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Mouthpart palp sensilla of basal Trichoptera families

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Abstract

A comparative SEM study of palp sensory surfaces in 25 caddisfly species representing seven families reveals seven types of sensilla: long trichoid, blunt chaetoid, campaniform, mushroom-like pseudoplacoid, petaloid, thick basiconic and thin basiconic sensilla. Long trichoid and chaetoid sensilla are present on all segments of both pairs of palps. First and second segments of maxillary palps bear groups of long and sclerotised chaetoid sensilla on their medial surface. Other segments of maxillary palps and all segments of labial palps have shorter and thinner chaetoid sensilla mainly on their ventromedial surfaces. Campaniform sensilla usually occur on the first segment of labial palps and second segment of maxillary palps. Mushroom-like pseudoplacoid sensilla may occupy all palp segments or only distal ones. Petaloid sensilla form sensory fields on apical segments of both pairs of palps in most studied species. Thick basiconic sensilla occur only in apical sensory complexes on tips of maxillary and labial palps. A comparison with the Lepidoptera suggests the similarity in palp sensilla and conservative evolution of the palp surface. The reconstructed ground plan for the palp sensory surfaces in Trichoptera and Amphiesmenoptera is provided.

Key Words

Amphiesmenoptera, evolution, labial palp, maxillary palp, sensilla, structure

Introduction

Sensory structures of insects are an important part of their nervous systems; a century of intensive explorations of their morphology and physiology resulted in a large amount of data overviewed in previous publications (e.g. Slifer (1970); Altner and Prillinger (1980); Zacharuk (1980); Ivanov (2000); Hallberg et al. (2003)). Some orders such as Lepidoptera, Diptera and Mecoptera attracted significant efforts of the researchers through the years (e.g. Faucheux (2005, 2008); Schneeberg and Beutel (2011); Lukashevich (2021); Wang et al. (2021) and references therein), but Trichoptera comparing to other insects have received less attention and little scientific knowledge has been reported previously on the sensilla on the mouthparts of caddisflies.

The Trichoptera palp segment numbers were discussed in connection with taxonomy of caddisflies since the pioneering publications by Kolenati (1851, 1859) who based his subordinal division of Trichoptera on the male palp segment number. More than 70 years later, the Trichoptera specialists returned to palp structures when Martynov (1924) proposed a new subordinal classification of caddisflies, based on additional characters, but including some characteristics of the maxillary and labial palps. This new system erected the suborders Annulipalpia, with annulated terminal palp segments and Integripalpia, usually without annulation. In these initial works, the palp sensilla were not discussed because of the lack of adequate morphological techniques to observe the fine structure of sensilla; minimal attention to sensory structures is apparent even in more recent publications on head morphology (Klemm 1966; Kubiak et al. 2015). Progress in scanning electron microscopy and understanding of the importance of fine sensory structures for taxonomy and communication studies resulted in wider exploration of the Trichoptera

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sensilla, mostly on the antennal segments (Ljungberg and Hallberg 1992; Ivanov and Melnitsky 2016; Ivanov et al. 2018; Melnitsky et al. 2018, 2019; Yuvaraj et al. 2018; Valuyskiy et al. 2020). For example, data obtained in studies of apical regions of palps (Ljungberg and Hallberg 1992; Ivanov et al. 2018) provided information on diversity of sensilla located in apical palp sensory complexes and, in comparison with the character set of Trichoptera suborders, suggested important arguments supporting the paraphyly of Spicipalpia (Ivanov 1997).

Preliminary assessment of the palp sensilla in Trichoptera (Ljungberg and Hallberg 1992), based on 23 species from 16 families, suggested the presence of five types of sensilla. The terminology of sensilla used in their publication is eclectic, using the presence of pores for some sensilla types and the outline of the cuticular part for other types. The authors described sensilla chaetica (equal to both the trichoid and the chaetoid sensilla of the present study), sensilla campaniformia (the campaniform sensilla), apical cone complex with larger and smaller pegs (the apical sensory complex with thick basiconic sensilla) and wall-pore sensilla (the pseudoplacoid sensilla), poreless sensilla (the petaloid sensilla). In this work, we will use the nomenclature of sensilla and distribution types previously used for antennae (e.g. Valuyskiy et al. (2017, 2020); Melnitsky et al. (2019)) and based on the shape and size of the cuticular parts of sensilla. This approach provides more stable nomenclature and permits comparison with previously obtained data on the antennal receptors.

The structure and distribution of the palp sensilla appeared much more diverse than we initially expected to find on these tiny appendages. The principal problem in comparative studies of the palp sensory structures is the lack of knowledge about the ground plan of palp surfaces and putative initial set of sensilla on these appendages. Comparative study of the palp sensilla in several *Rhyacophila* species (Abu Diiak et al. in press) suggested a rather constant sensilla set and limited variations in size and numbers within a large and diverse, primitive genus of Trichoptera. We will use the previously obtained data on this genus as a background and include only few previously unexplored Rhyacophilidae species in the current study.

Our investigations of fine external structure and distribution are targeted on the comparative study of basal families as indicated by current phylogenies (Holzenthal et al. 2007b; Thomas et al. 2020). The families Philopotamidae and Stenopsychidae in our material represent the Annulipalpia, the rest of them belonging to the Integripalpia sensu lato with Rhyacophilidae probably representing the most generalised adults amongst all modern Trichoptera. Additional data on the family Rhyacophilidae are published elsewhere (Abu Diiak et al. in press).

The purpose of this paper is to describe the sensory structures in seven basal families of Trichoptera (Thomas et al. 2020). A comparison with outgroups (Lepidoptera and Mecoptera) provides insight in the ground plan of the palp sensory surfaces in relation to the sensilla diversity and distribution. We also compare the sensilla on palps to those on antennae to find the opportunity for palp sensilla to substitute or to complement the antennal sensilla in certain situations, for example, in mating communication.

Materials and methods

The palp sensory structures of 25 species from seven families of caddisflies were observed (including those of both sexes indicated with *): **Himalopsyche acharai* Malicky & Chantaramongkol, 1989 (Thailand); *Rhyacophila impar* Martynov, 1914 (Russia, Siberia); and **Rh. munda* McLachlan, 1862 (Morocco) (Rhyacophilidae); **Glossosoma unguiculatum* Martynov, 1925 (Georgia); **G. altaicum* (Martynov, 1914) (Russia, Siberia); **G. schmidi* (Levanidova, 1979) (Russian Far East); **Agapetus sindis* Kimmins, 1953 (Tajikistan); *Agapetus fuscipes* Curtis, 1834 (France); **Synagapetus oblongatus* Martynov, 1913 (Russia, Caucasus); and *Padunia adelungi* Martynov, 1910 (Russia, Siberia) (Glossosomatidae); **Hydroptila cornuta* Mosely, 1922 (Russia, Caucasus); **Oxyethira falcata* Morton, 1893 (Russia, Caucasus); **Orthotrichia costalis* (Curtis, 1834) (Northwest of European Russia); and **Agraylea sexmaculata* Curtis, 1834 (Russia, Caucasus) (Hydroptilidae); **Ptilocolepus colchicus* Martynov, 1913 (Russia, Caucasus) (Ptilocolepidae); *Apsilochorema sutchanum* Martynov, 1934 (Russian Far East); **Taschorema apobamum* Neboiss, 1977 (Australia, Tasmania); and *Ulmerochorema stigmum* (Ulmer, 1916) (Australia, New South Wales) (Hydrobiosidae); *Philopotamus montanus* (Donovan, 1813) (North of European Russia); **Dolophilodes ornata* Ulmer, 1909 (Kazakhstan); **Wormaldia khourmai* Schmid, 1959 (Russia, Caucasus); **Chimarra marginata* (Linnaeus, 1767) (Northwest of European Russia); *Chimarra thienemanni* Ulmer, 1951 (Thailand); and *Chimarra okuihorum* Mey, 1998 (Malaysia) (Philopotamidae); *Stenopsyche marmorata* Navas, 1920 (Russian Far East) (Stenopsychidae). Additionally, two representatives of basal Lepidoptera were investigated for comparison: **Micropterix maschukella* Alpheraky, 1876 (Southwest of European Russia) (Micropterigidae) and **Eriocrania cicatricella* (Zetterstedt, 1839) (Northwest of European Russia) (Eriocraniidae). The material examined was obtained from the collection of the Department of Entomology of St. Petersburg State University. All insects used in this study were stored in 70% ethanol.

Observations were made using scanning electron microscopy (SEM). The palps or heads were removed, dried, mounted on specimen holders and covered with 20 nm gold coating in Leica EM SCD500. The micrographs were taken with Tescan MIRA3, Hitachi TM3000 and FEI Quanta 200 3D scanning electron microscopes. All equipment was provided by the Resource Centers of St. Petersburg State University: "Development of Molecular and Cellular Technologies" and "Resource Center for Microscopy and Microanalysis." Counting and measurements of the sensilla on the photographs were made with the ImageJ 1.52r software.

Results

Structure of palp segments

The cuticle of the palp segments of Trichoptera is usually firm structurally, but the sclerotisation of joints is weaker for better flexibility. Certain areas of segments bearing assemblages of sensilla (often covered by peculiar groups of sensilla, the sensory fields) have thinner and more flexible cuticle resulting in large-scale deformations on dry preparations ready for SEM. The distal parts of all palp segments, except apical ones, are obliquely truncated and bear a subapical excision allowing a broader range of motion. Almost all the surfaces of the palps, excepting articulations and specialised terminal areas, are covered with microtrichia (Figs 1–3). The latter are small non-innervated processes which do not perform sensory functions. The surfaces of apical segments of Philopotamidae and Stenopsychidae bear numerous transverse cuticular folds (Fig. 2D). These folds produce an appearance of annulations of segments which is a synapomorphic character of the Annulipalpia; the SEM photographs show numerous irregularities in the folds, sometimes producing mesh-like structures (Fig. 2D).

Labial palps of examined Trichoptera are three-segmented (Fig. 2A–C), and maxillary palps are five-segmented (Fig. 3A–D). The first and second segments of labial palps are approximately equal in length. These segments are almost cylindrical with slightly narrowed base. The third segment is 1.5–3.0 times longer than the first or second segment.

Maxillary palps of examined caddisflies are longer than labial palps. The first and second segments of maxillary palps are the shortest and usually equal in length, with the first segment cylindrical and the second more nearly globular (Fig. 3A). Sometimes the second segment is 1.5–3.0 times longer than the first and has a cylindrical shape (Hydrobiosidae and Philopotamidae, except *W. khourmai*). Third, fourth and fifth segments are elongate and cylindrical. In most examined species, the third and fifth segments are equal in length, whereas the fifth segment of *Ph. montanus* and *S. marmorata* is strongly elongated and is 2–3 times as long as the third segment. The fourth segment is usually 1.5–3.0 times shorter than the third and fifth. In some cases, it has nearly the same length as these segments [e.g. Hydrobiosidae, Hydroptilidae, Ptilocolepidae (*P. colchicus*) and Rhyacophilidae (*H. acharai*)].

Examined maxillary and labial palps of Lepidoptera have the same number of segments as in Trichoptera (five and three, respectively). All three segments of labial palps are cylindrical and approximately equal in length. Segments of maxillary palps are also cylindrical. All palp segments of *E. cicatricella* (Eriocraniidae) and most segments of *M. maschukella* (Micropterigidae) are covered with microtrichia, whereas the first segment of each labial palp and the fifth segment of each maxillary palp of the latter lack microtrichia. The fifth maxillary palp segment of *M. maschukella* has pronounced longitudinal cuticular ridges (Fig. 3F), but its fourth maxillary palp segment is covered with transverse cuticular folds.

Structure and diversity of sensilla

The classification of sensilla used in this work was previously suggested by Ivanov et al. (2018). We have observed seven types of sensilla on the maxillary and labial palps of studied species. Minimal and maximal sizes of various types of sensilla are given in Tables 1, 2.

Long trichoid sensilla (*lts*: Figs 1A, B, D, L, 2A–D, 3A–E, 4A) are randomly (non-specifically) distributed over all segments of maxillary and labial palps of all specimens examined. All studied caddisflies possess one subtype of this sensilla type, the pointed trichoid sensilla (Fig. 1A, B). They have a flattened elongated shape, acute tips and longitudinal ridges and serration on dorsal surfaces. This serration is most pronounced in Hydroptilidae, where long trichoid sensilla are covered with numerous pointed processes (Fig. 1B).

We consider moth scales as homologues of the long trichoid sensilla. Some of these structures might be innervated and, in this instance, can be designated as scale-shaped long trichoid sensilla. Long trichoid sensilla are easily detached, leaving empty, elongated sockets. Some of these structures might be scales without sensory function; a histological study is necessary to discriminate these two types of sensilla and, presently, we consider all of them to be sensory structures until future research might provide additional information on their functions.

Maxillary and labial palps of Lepidoptera *M. maschukella* and *E. cicatricella* bear pointed, long trichoid sensilla in addition to scales and scale-shaped sensilla (*sc*). The latter are wider and flatter structures with deep longitudinal grooves (Fig. 1C). The long trichoid sensilla and scales occur on all segments of maxillary and labial palps (except the fifth segment of maxillary palps in *M. maschukella*) and are non-specifically distributed.

Blunt chaetoid sensilla (*chs*: Figs 1D–E, 2A–D, 3A–E, 4A) were found on all segments of both pairs of palps in all studied species. These sensilla are hair-shaped structures, each with a round cross section, longitudinal striation and blunt tip. Palps of Trichoptera have two subtypes of these sensilla: Long (*chs-l*) and short (*chs-s*). Long and sclerotised blunt chaetoid sensilla with rounded or bean-shaped sockets (the latter sometimes with elevated ridges produced by raised socket walls limiting the movement in a short range and one direction) occur in dense groups on medial surfaces of the first and second segments of maxillary palps (Figs 1E, 3A, E). They are upright and, if inclined, can incline towards the surface of a segment directed by their socket walls. Sensilla of this type do not form such groups in Hydrobiosidae, *P. adelungi* (Glossosomatidae) and *A. sexmaculata* (Hydroptilidae). Species of the genus *Chimarra* (Philopotamidae) have these sensilla only on distal parts of the second segments of

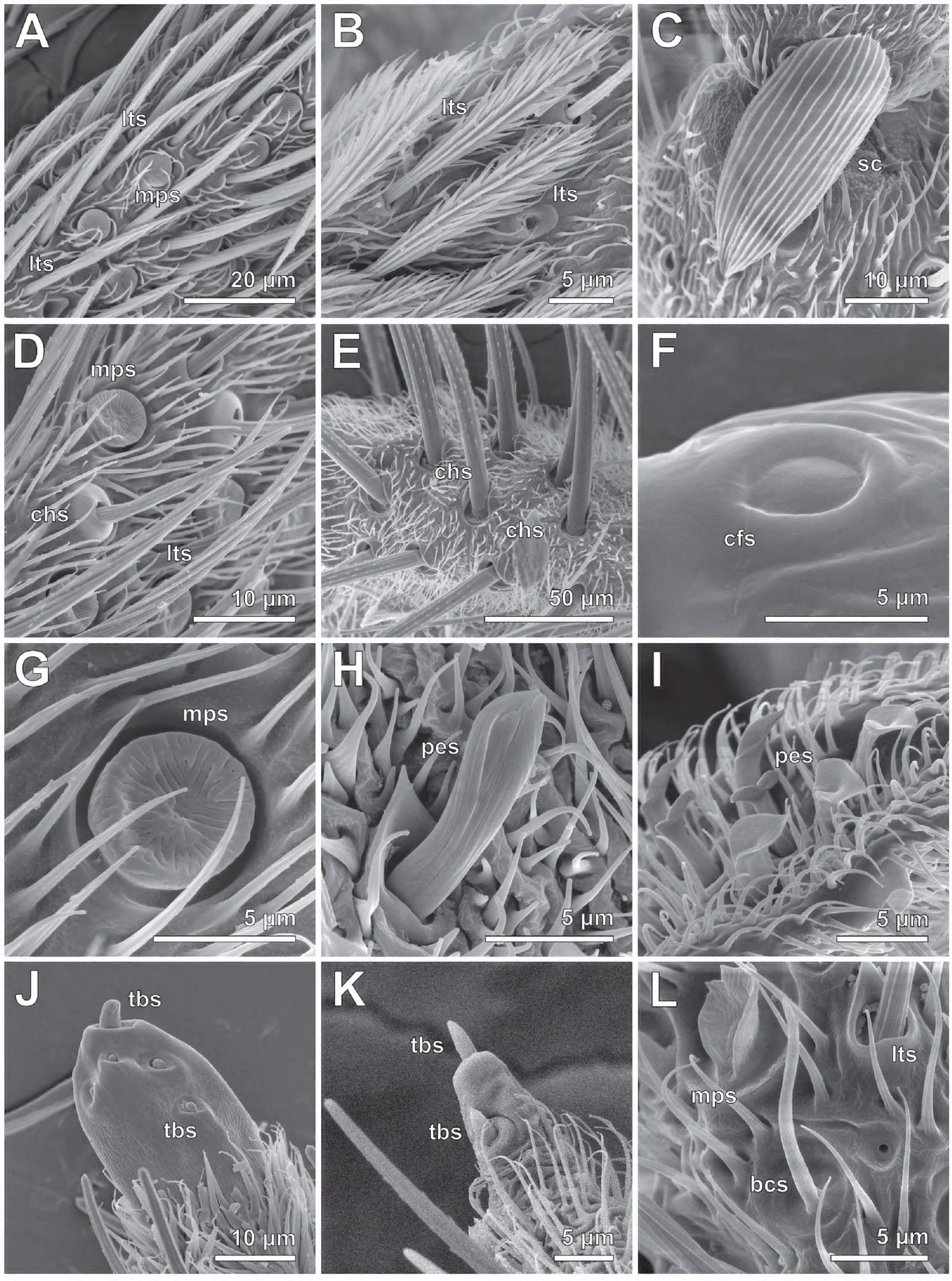

Figure 1. Sensilla of maxillary and labial palps of Trichoptera and Lepidoptera. **A.** Lateral surface third segment of maxillary palp in *D. ornata* male; **B.** Long trichoid sensilla on the third segment of labial palp in *O. falcata* female; **C.** Scale-shaped long trichoid sensillum on the third segment of labial palp in *M. maschukella* male; **D.** Chaetoid sensillum on the fourth segment of maxillary palp in *Ch. marginata* male; **E.** Bases of chaetoid sensilla on the second segment of maxillary palp in *Rh. munda* male; **F.** Campaniform sensillum on the fifth segment of maxillary palp in *M. maschukella* female; **G.** Mushroom-like pseudoplacoid sensillum on the third segment of maxillary palp in *Ch. marginata* male; **H.** Petaloid sensillum on the third segment of labial palp in *Rh. impar* male; **I.** Petaloid sensilla on the third segment of labial palp in *H. cornuta* female; **J.** Apical sensory complex on the third segment of labial palp in *Rh. impar* male; **K.** Apical sensory complex on the third segment of labial palp in *G. schmidi* female; **L.** Thin basiconic sensillum on the fifth segment of maxillary palp in *G. altaicum* male. Abbreviations: **bcs** = thin basiconic sensilla; **cfs** = campaniform sensilla; **chs** = blunt chaetoid sensilla; **lts** = pointed long trichoid sensilla; **mps** = mushroom-like pseudoplacoid sensilla; **pes** = petaloid sensilla; **sc** = scale; **tbs** = thick basiconic sensilla.

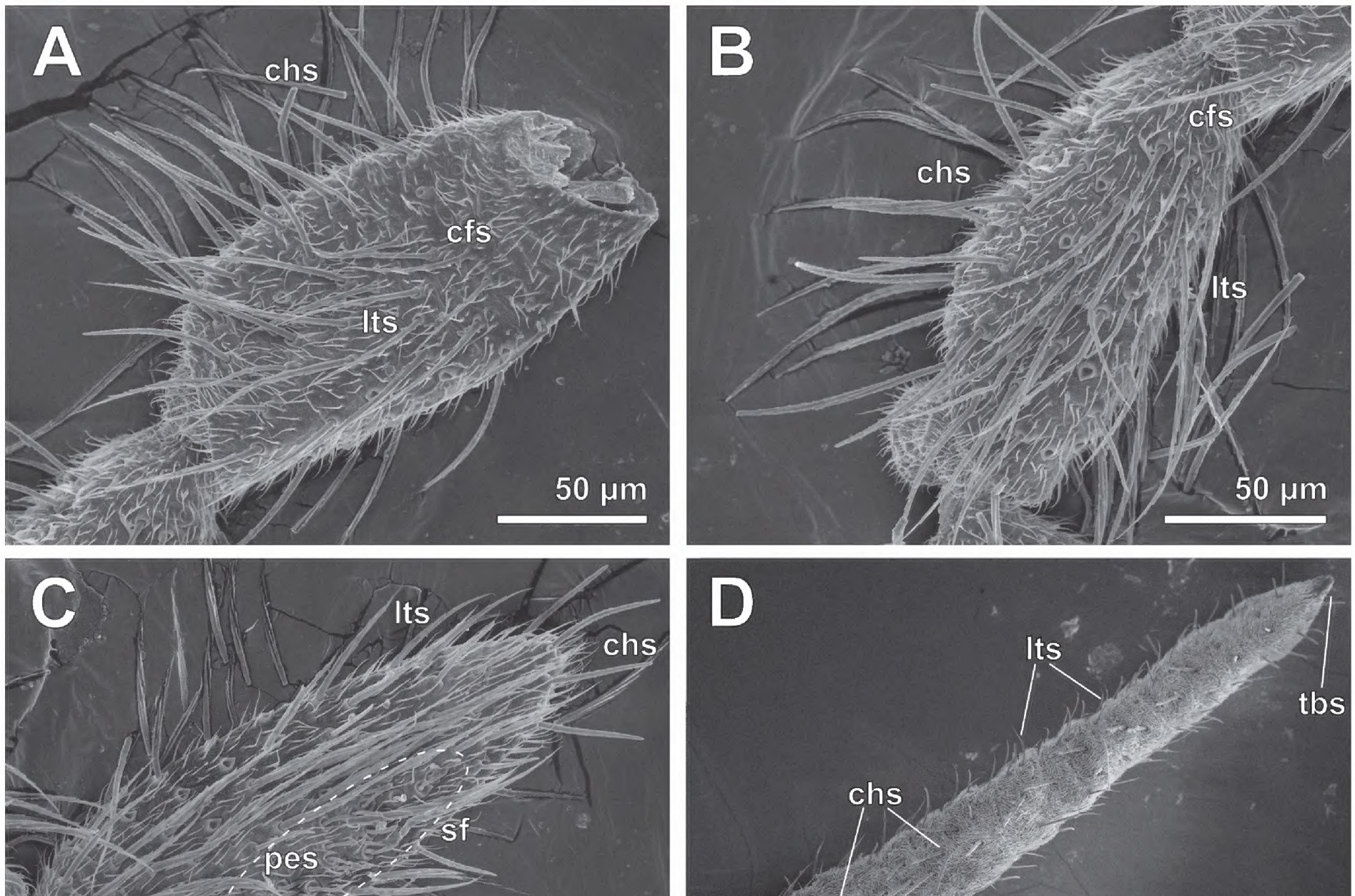

Figure 2. Labial palps of Trichoptera and Lepidoptera. **A–C.** first, second and third labial palp segments of *A. sutchanum* male; **D.** third labial palp segment of *S. marmorata* male; **E.** Sensory field of petaloid sensilla on the third labial palp segment of *S. marmorata* male; **F.** Apical part of third labial palp segment of *M. maschukella* male. Abbreviations: **cfs** = campaniform sensilla; **chs** = blunt chaetoid sensilla; **lts** = pointed long trichoid sensilla; **mps** = mushroom-like pseudoplacoid sensilla; **pes** = petaloid sensilla; **s** = empty socket of long trichoid sensilla; **sc** = scale; **sf** = sensory field; **tbs** = thick basiconic sensilla.

maxillary palps (Fig. 3E). Short and weakly sclerotised blunt chaetoid sensilla (Fig. 1D) are present on all segments of maxillary and labial palps (Figs 2, 3A–E). The highest density of these thin chaetoid sensilla is observed on medial and ventral surfaces of third–fifth segments of maxillary and labial palp segments.

The studied moths have significant differences from caddisflies in distribution of blunt chaetoid sensilla.

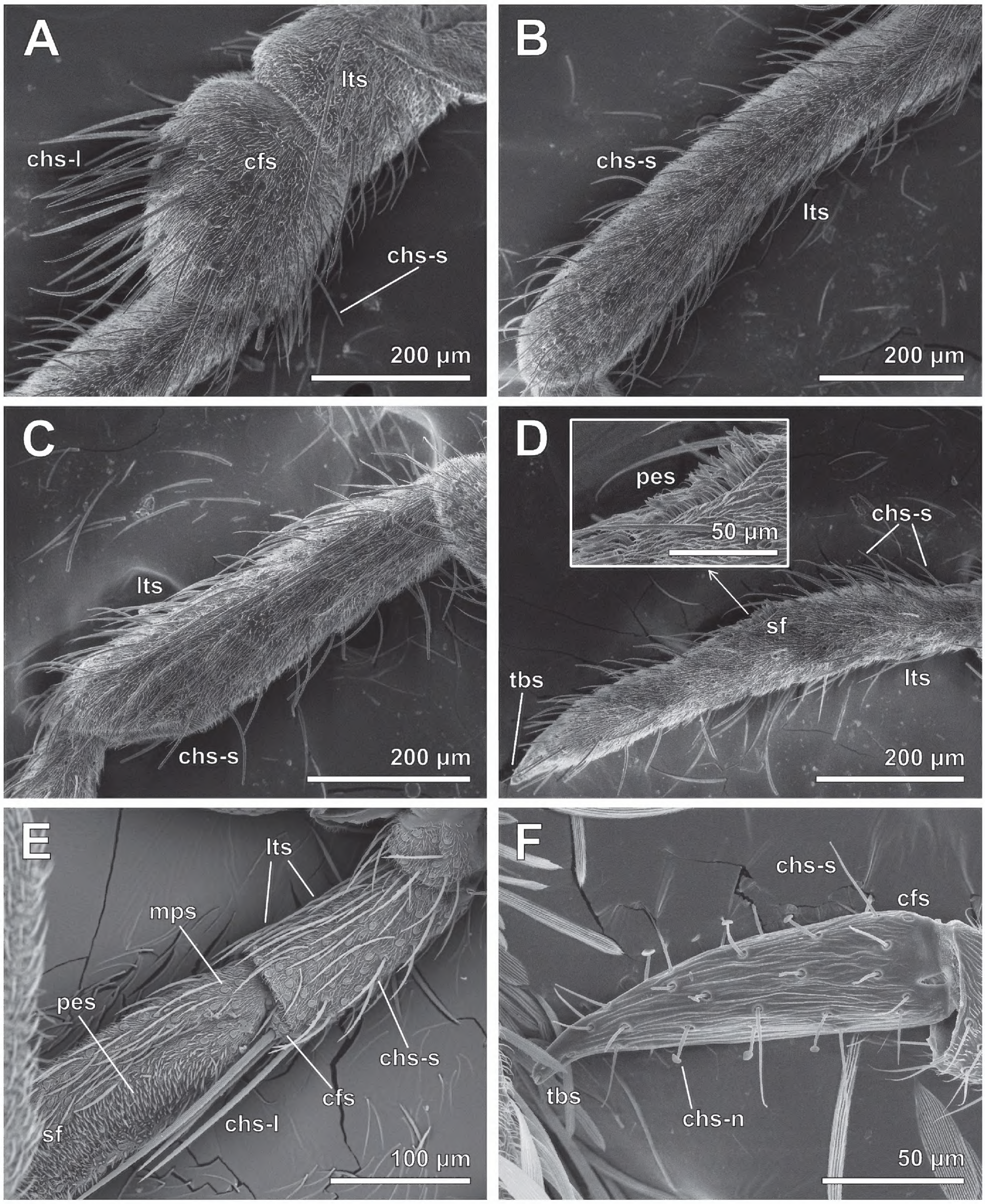

Figure 3. Maxillary palps of Trichoptera and Lepidoptera. **A.** First and second maxillary palp segments of *H. acharai* male; **B–D.** Third, fourth and fifth maxillary palp segments of *H. acharai* male; **E.** First, second and third maxillary palp segments of *Ch. thienemanni* male; **F.** Fifth maxillary palp segment of *M. maschukella* female. Abbreviations: **cfs** = campaniform sensilla; **chs-l** = longer blunt chaetoid sensilla; **chs-n** = nail-shaped chaetoid sensilla; **chs-s** = shorter blunt chaetoid sensilla; **lts** = pointed long trichoid sensilla; **mps** = mushroom-like pseudoplacoid sensilla; **pes** = petaloid sensilla; **sf** = sensory field; **tbs** = thick basiconic sensilla.

Sensilla of this type are very scarce on maxillary and labial palps of *E. cicatricella*, whereas *M. maschukella* has dense groups of blunt chaetoid sensilla on ventromedial surfaces of second–third labial palp segments (Fig. 2F) and first–second maxillary palp segments. The fifth segments of maxillary palps in *M. maschukella* also

Table 1. Length variation (μm) of labial palp sensilla in males of studied Trichoptera. Abbreviations: **Min** = minimum length, **Max** = maximum length, **lts** = long trichoid sensilla, **chs-s** = short chaetoid sensilla, **mps** = mushroom-like pseudoplacoid sensilla, **pes** = petaloid sensilla. Family numbers: **1** = Rhyacophilidae (*Himalopsyche*, *Rhyacophila*), **2** = Glossosomatidae (*Glossosoma*, *Agapetus*, *Synagapetus*, *Padunia*), **3** = Hydroptilidae (*Agraylea*, *Hydroptila*, *Orthotrichia*, *Oxyethira*), **4** = Ptilocolepidae (*Ptilocolepus*), **5** = Hydrobiosidae (*Apsilochorema*, *Taschorema*, *Ulmerochorema*), **6** = Philopotamidae (*Chimarra*, *Dolophilodes*, *Philopotamus*, *Wormaldia*), **7** = Stenopsychidae (*Stenopsyche*).

Families (numbers) and species		Lts		chs-s		mps		pes	
		Min	**Max**	**Min**	**Max**	**Min**	**Max**	**Min**	**Max**
1	*H. acharai*	33.1	112.0	23.4	79.1	–	–	16.3	19.2
	Rh. impar	50.2	58.9	26.0	60.4	4.6	7.2	8.7	10.7
	Rh. munda	42.7	89.2	38.3	77.7	4.2	4.9	–	–
2	*G. unguiculatum*	26.1	29.7	11.8	42.6	5.1	5.7	5.3	7.5
	G. altaicum	23.2	48.9	15.7	44.4	4.6	5.5	5.6	8.9
	G. schmidi	47.3	60.6	10.2	53.8	5.2	5.3	5.3	6.2
	A. sindis	29.4	45.3	13.2	41.9	–	–	–	–
	A. fuscipes	22.5	43.9	17.6	31.3	–	–	6.9	8.5
	P. adelungi	34.1	35.0	8.8	25.0	4.3	4.3	–	–
3	*H. cornuta*	20.2	35.2	9.6	34.9	–	–	6.4	7.0
	O. falcata	20.6	34.3	11.4	25.6	–	–	4.5	4.8
	O. costalis	11.9	28.1	7.8	24.1	–	–	3.7	4.3
	A. sexmaculata	31.9	31.9	19.0	19.0	–	–	7.2	10.0
4	*P. colchicus*	76.1	90.0	24.3	41.8	–	–	–	–
5	*A. sutchanum*	43.9	72.6	20.6	90.0	–	–	10.2	11.7
	T. apobamum	35.8	44.1	16.1	83.4	–	–	13.9	14.5
	U. stigmum	24.7	49.5	14.0	58.8	–	–	–	–
6	*P. montanus*	24.5	65.1	17.6	93.5	7.7	8.7	7.1	8.4
	D. ornata	16.4	44.1	14.6	40.5	5.9	6.7	4.4	6.6
	W. khourmai	24.0	56.2	16.1	58.2	5.3	7.1	–	–
	Ch. marginata	17.6	64.1	15.4	54.3	5.3	6.5	–	–
	Ch. thienemanni	14.8	37.0	12.9	44.7	4.6	7.0	4.5	5.3
	Ch. okuihorum	12.3	30.5	12.3	44.8	6.8	8.7	–	–
7	*S. marmorata*	21.8	78.8	21.0	132.3	–	–	9.4	10.1

Table 2. Length variation (μm) of maxillary palp sensilla in males of studied Trichoptera.

Families (numbers) and species		lts		chs-s		chs-l		mps		pes	
		Min	**Max**	**Min**	**Max**	**Min**	**Max**	**Min**	**Max**	**Min**	**Max**
1	*H. acharai*	42.4	114.7	59.1	100.2	145.3	147.3	–	–	13.6	15.6
	Rh. impar	40.3	84.0	24.3	67.9	130.2	140.1	5.0	7.0	11.4	14.3
	Rh. munda	72.7	104.8	35.1	47.9	180.4	389.3	4.2	5.0	8.4	10.1
2	*G. unguiculatum*	23.3	40.9	17.7	64.2	95.0	96.5	3.1	8.4	–	–
	G. altaicum	29.9	47.6	15.0	51.0	82.2	143.2	4.5	7.0	–	–
	G. schmidi	31.1	65.5	20.0	50.1	92.5	109.2	5.2	9.2	–	–
	A. sindis	26.7	50.0	8.9	32.5	29.6	33.1	6.1	6.1	–	–
	A. fuscipes	34.1	64.0	10.4	37.4	29.2	35.6	3.3	4.8	–	–
	S. oblongatus	27.1	62.6	10.7	31.1	35.4	37.6	6.3	7.3	–	–
	P. adelungi	31.3	42.8	13.8	15.6	–	–	2.7	3.8	–	–
3	*H. cornuta*	16.4	49.3	11.7	34.2	57.4	121.2	–	–	–	–
	Ox. falcata	16.9	32.4	10.8	33.9	65.0	96.2	–	–	–	–
	Or. costalis	12.5	56.1	7.3	33.8	–	–	–	–	–	–
	A. sexmaculata	19.6	37.0	11.6	19.3	–	–	–	–	–	–
4	*P. colchicus*	30.9	118.4	23.9	69.8	26.4	26.4	–	–	–	–
5	*A. sutchanum*	37.2	97.8	19.5	69.0	44.9	89.6	–	–	–	–
	T. apobamum	39.0	191.7	11.4	110.2	123.4	139.0	–	–	–	–
	U. stigmum	31.2	67.4	20.3	62.5	58.8	66.4	–	–	9.8	12.7
6	*P. montanus*	23.9	154.4	13.0	114.9	154.4	243.2	7.9	9.8	–	–
	D. ornata	15.1	65.1	13.8	78.9	56.5	110.2	4.9	7.0	–	–
	W. khourmai	16.5	88.9	11.2	62.8	77.5	109.3	4.4	6.7	–	–
	Ch. marginata	18.7	41.2	14.3	39.3	119.4	312.7	5.8	6.7	–	–
	Ch. thienemanni	12.5	54.7	15.6	59.1	138.3	204.8	5.3	7.8	4.7	10.3
	Ch. okuihorum	20.0	54.1	14.7	58.3	63.8	166.9	6.6	10.7	4.6	6.6
7	*S. marmorata*	22.9	118.6	21.8	125.2	141.5	257.6	–	–	–	–

Abbreviations: **Min** = minimal, **Max** = maximal length, **lts** = long trichoid sensilla, **chs-s** = short chaetoid sensilla, **chs-l** = long blunt chaetoid sensilla, **mps** = mushroom-like pseudoplacoid sensilla, **pes** = petaloid sensilla. Family numbers: **1** = Rhyacophilidae (*Himalopsyche*, *Rhyacophila*), **2** = Glossosomatidae (*Glossosoma*, *Agapetus*, *Synagapetus*, *Padunia*), **3** = Hydroptilidae (*Agraylea*, *Hydroptila*, *Orthotrichia*, *Oxyethira*), **4** = Ptilocolepidae (*Ptilocolepus*), **5** = Hydrobiosidae (*Apsilochorema*, *Taschorema*, *Ulmerochorema*), **6** = Philopotamidae (*Chimarra*, *Dolophilodes*, *Philopotamus*, *Wormaldia*), **7** = Stenopsychidae (*Stenopsyche*).

bears sensilla of this subtype along with nail-shaped (*chs-n*) chaetoid sensilla (Fig. 3F). The latter resemble blunt chaetoid sensilla, but their tips bear small rounded plates. Despite the presence of terminal plates in these sensilla resembling the caps of mushroom-like pseudoplacoid sensilla, we consider them as a nail-shaped subtype of chaetoid sensilla because of the structure of their sockets, permitting movement apparently similar to those of other chaetoid sensilla and because these sensilla are much longer and more sclerotised, similar to chaetoid sensilla.

Campaniform sensilla (*cfs*: Figs 1F, 2A, 3A, E, F, 4A) each have a thin flat or dome-shaped cuticular area surrounded by an elevated cuticular ring. These structures occur sporadically on the first segment of labial palps and the second segment of maxillary palps (singly or in groups of up to five sensilla). Sometimes solitary campaniform sensilla can be found on other segments. The diameter of the internal region inside the cuticular ring of these sensilla usually varies from 2.5 to 5 μm.

Mushroom-like pseudoplacoid sensilla (*mps*: Figs 1A, D, G, L, 2F, 3E, 4A) are present in all representatives of the families Philopotamidae and Glossosomatidae, as well as in some Rhyacopilidae (*Rh. impar*, *Rh. munda*). Sensilla of this type occur on both maxillary and labial palps, with a tendency to be more numerous on dorsal surfaces. They each have a rounded or flattened wider apical part forming a cap as in a mushroom, which is positioned on a thick and short, unmovable stem. Their apical surfaces have pore-bearing grooves diverging from the centre. These sensilla are slightly elongated distad in *D. ornata* (Philopotamidae) (Fig. 1A) and most Glossosomatidae, except for *A. sindis*, *A. fuscipes* and *S. oblongatus* (Fig. 1L). Mushroom-like pseudoplacoid sensilla are non-specifically distributed over all segments of both pairs of palps in Philopotamidae. Glossosomatidae have these sensilla on each fifth maxillary palp segment in *P. adelungi*, *A. sindis*, *A. fuscipes* and *S. oblongatus*, on third–fifth segments of maxillary palps in *G. schmidi*, *G. unguiculatum* and *G. altaica* and on each third segment of labial palps in *P. adelungi* and *G. altaica*. The same sensilla in the studied Rhyacophilidae species occur across fourth–fifth segments of maxillary and second–third segments of labial palps in *Rh. impar* and on the third labial and fifth maxillary segments in *Rh. munda*. In the Lepidoptera, the mushroom-like pseudoplacoid sensilla occur in groups of 2–3 and are shifted ventrad from the apices of the third labial palp segments of *M. maschukella* (Fig. 2F) or are absent in the Eriocraniidae.

Petaloid sensilla (*pes*: Figs 1H, I, 2C–F, 3D, E, 4A) were found in all studied species, except for *P. adelungi* and *A. sindis* (Glossosomatidae) and *W. khourmai* and *Ch. marginata* (Philopotamidae). This type of sensilla comprises two subtypes: curved petaloid sensilla (Fig. 1H) and flattened petaloid sensilla (Fig. 1I). Most studied species, except for Rhyacophilidae, Hydrobiosidae and the genus *Chimarra* (Philopotamidae), possess flattened petaloid sensilla. These structures each have a wide flat apical plate attached almost at a right angle to a slender stem. Curved petaloid sensilla were noted for Rhyacophilidae, Hydrobiosidae and species of the genus *Chimarra*. These are elongate, curved and pointed structures with slight spiral grooves.

Sensory fields (*sf*) are specific areas covered exclusively with petaloid sensilla on palps of the studied species (Figs 2C–F, 3D, E, 4B, C). These areas are present in 19 caddisfly species on the labial palps (except they are not in *P. adelungi*, *A. sindis*, *U. stigma*, *W. khourmai*, *Ch. marginata* and *Ch. okuihorum*) and on the maxillary palps of seven species (*Rh. impar*, *Rh. munda*, *H. acharai*, *U. stigma*, *T. apobamum*, *Ch. thienemanni* and *Ch. okuihorum*). Sensory fields are usually oval-shaped or strip-shaped. In some species, sensory fields are extremely long and wide, occupying half of the segment surface (e.g. on maxillary palps of *Ch. thienemanni* and labial palps of *A. sexmaculata*). Sensory fields of labial palps are always located on the third segment (Fig. 2C–F), whereas sensory fields of maxillary palps may be located on the fifth segment as in *Rh. impar*, *Rh. munda*, *H. acharai*, *U. stigma* and *T. apobamum* (Fig. 3D) or on the third segment as in species of *Chimarra* (Fig. 3E). The position of these fields on the segment is very variable within the studied species: they may occur ventrally in Glossosomatidae, Hydroptilidae, *P. colchicus*, *D. ornata* and *P. montanus*, dorsally in Rhyacophilidae and Hydrobiosidae, medially in *Ch. thienemanni* and *S. marmorata* and laterally in *Ch. okuihorum*. The number of petaloid sensilla in sensory fields on maxillary palps varies from 21 in *Ch. okuihorum* to 460 in *Ch. thienemanni* (Fig. 3E); on labial palps from seven in *G. unguiculatum* to 140 in *A. sexmaculata*. Sensory fields observed in Lepidoptera are visible as depressions on the third segment of labial palps provided with 15–20 petaloid sensilla nested inside the depression (Fig. 2F). These depressions each have a subapical morphologically dorsal position.

Thick basiconic sensilla (*tbs*: Figs 1J, K, 2D, 3D–F, 4A) occur only as part of apical sensory complexes– smooth, poreless projections positioned on tips of terminal segments of maxillary and labial palps. These sensilla can be described as small, cone-shaped, poreless structures; sometimes an apical thick basiconic sensillum bears longitudinal grooves (e.g. in *Rh. impar*, *G. unguiculatum*, *G. altaicum* and *P. colchicus*). Sensilla of this type are present in the majority of the studied species, except not in species of the genus *Chimarra* (Philopotamidae), some Glossosomatidae (e.g. *P. adelungi*, *S. oblongatus* and *A. sindis*), most Hydrobiosidae (except present in *T. apobamum*) and Hydroptilidae.

The apices of both pairs of palps observed in most Trichoptera bear specialised apical sensory complexes. These are slightly elongated outgrowths with smooth surfaces (Fig. 1J, K). Microtrichia which cover almost the whole surface of palp segments are completely absent from apical sensory complexes. Each apical sensory complex bears only thick basiconic sensilla which are present only within such complexes. The apical thick basiconic sensillum is the longest within the complex, usually exceeding 3 μm in length; lateral sides of each complex are

covered with 2–5 shorter sensilla, each usually less than 2 μm, of the same type. Lateral thick basiconic sensilla of *P. colchicus* and *T. apobamum* measuring from 3 to 4 μm are much longer than in other species. Lepidoptera examined have apical sensory complexes of thick basiconic sensilla on the fifth segments of maxillary palps. There is only one apical, thick basiconic sensillum in the apical sensory complex of *M. maschukella* and a few smaller subapical ones (Fig. 3F), whereas the apical sensory complexes of *E. cicatricella* have 4–5 almost equal apical sensilla. The apical sensory complex in Lepidoptera is more or less separated from the rest of the terminal palp segment, but in Trichoptera, there is a distinct border between the surface of the thick apical segment and the much thinner apical complex. The terminal maxillary segments in Micropterigidae and Eriocraniidae examined have a smooth transition to these complexes. The border of this complex in Lepidoptera is visible in the change of segment surface: it is always smooth in the terminal complex, contrary to other segment surfaces having microtrichia or longitudinal ridges.

Thin basiconic sensilla (*bcs*: Fig. 1L) were found only on the fourth and fifth segments of maxillary palps in *G. altaica*. These are short and slender peg-like structures with slight spiral striation. Their bases are fused with a surrounding cuticle. The length of these sensilla varies over 6–12 μm.

Discussion

The typical set of sensilla on the palps is represented by six main types and two subtypes differing in size and sclerotisation, namely, the long dark blunt chaetoid (gustatory) sensilla and the short, light, thin-walled sensilla. All these types and subtypes are universal in Trichoptera palps, widespread and indicate the similarity of palp functions in different species. The remaining type, thin basiconic sensilla, have been observed only in one species, *G. altaicum*.

A comparison with sensilla on the antenna of the same species (Ivanov and Melnitsky 2011, 2016; Valuyskiy et al. 2017; Melnitsky et al. 2018) shows the reduced and altered variety of sensilla on palps. For example, the antennae of Rhyacophilidae often have several subtypes of pseudoplacoid sensilla (Valuyskiy et al. 2017), but the occurrence of multiple subtypes of pseudoplacoid sensilla was never found on palps (Abu Diiak et al. in press and the present study). The thin curved trichoid sensilla and Böhm's bristles persistent on the antenna of various Trichoptera are not found on palps. The thick basiconic and petaloid sensilla characteristic for palps, conversely, were not found on antennae. The diversity of pseudoplacoid sensilla on palps are limited mostly to the ubiquitous mushroom-like subtype. The similarity of the palp sensory surfaces in various basal families is notable; we refrain from detailed descriptions of the sensilla types and distribution in every studied species because such descriptions would be mostly repetitious.

There are great similarities in types, number and distribution of sensilla in basal families; therefore, these parameters are mostly uninformative for diagnosis or phylogeny. For example, the exceptional multiplication of pseudoplacoid sensilla on all segments of palps in the Philopotamidae species might be specific for this family, but does not characterise the Annulipalpia because Stenopsychidae lack these sensilla. Consistent fluctuations in subtypes, degree of development, presence or absence of certain types of sensilla are possible at lower taxonomic levels. We found structural variations of the apical sensory complexes, various development of the pseudoplacoid sensilla on palps of Rhyacophilidae and other families and differences in petaloid sensilla and sensory fields covered by them, but in most instances, these were variations of less-inclusive taxonomic levels, characterising only certain species. Similar deviations have been encountered before in Rhyacophilidae (Abu Diiak et al. in press). These deviations might be important for less-inclusive taxonomic levels, like genus and subfamily, but are uninformative for family-level diagnosis or phylogeny. The sensory surfaces of mouthpart palps look very conservative with some slight variations for species adaptation. Nonetheless, we found the abundant coverage of pseudoplacoid sensilla on second–fifth segments in Philopotamidae to be a probable characteristic for the whole family. Contrary to expectations, the families Rhyacopilidae and Hydrobiosidae are significantly different in the complete absence of pseudoplacoid sensilla on the palps of the latter. The apical sensory complexes were observed in all Rhyacophilidae, but were absent in Hydrobiosidae, except for the labial palps of *T. apobamum*. The Ptilocolepidae, unlike their close relatives Hydroptilidae, have typical trichoid sensilla without modified heavy serration (Fig. 1B).

The development of peculiar "annulipalpian," long, annulated terminal segments on both maxillary and labial palps does not result in principal changes in sensilla distribution and is not correlated with evolution of new sensilla types. Apical sensory complexes persist in basal Annulipalpia (Ljungberg and Hallberg 1992; Ivanov et al. 2018), but look reduced in size and sensilla numbers. The ventral surfaces of the elongate fifth segments of maxillary palps and third segments of labial palps are provided with numerous blunt chaetoid upright sensilla in rows, probably serving as chemomechanoreceptors; they can scan substrate surfaces if the palps move laterally across them.

The two basal segments of the maxillary palps are often shortened in Trichoptera and both are provided with large, sclerotised chaetoid sensilla. These sensilla occur in groups on the medial surface and are inclined, appearing to be extended for touching a target between the palps. The enlarged second segment has an anteromedial swelling that might facilitate the function of these sensilla in accessing their stimuli. Its larger internal volume provides space for the neurons and accessory cells of these sensilla. In some instances (e.g. males of *Rh. munda*), the lengths of large chaetoid sensilla decrease in the anterior direction, collectively appearing to become a flat surface.

On the other hand, the thinner pale chaetoid sensilla on the ventral surface are positioned almost at right angles and are always short. We presume both types to be contact mechanochemoreceptors although they have different (albeit unstudied) functions. The swollen condition of the second segment disappears when the medial long sensilla are reduced, for example, in Hydrobiosidae, some Hydroptilidae and species of *Chimarra* (Fig. 3E).

The major tendencies in the development of sensilla in basal Trichoptera families can be described as reduction and subsequent loss of some structures that are possibly an ancestral state for the order. The apical sensory complexes belong to declining structures, decreasing in size and sensilla numbers in some Annulipalpia [Philopotamidae, Glossosomatidae (subfamily Glossosomatinae)] disappearing in other Glossosomatidae (subfamilies Agapetinae, Protoptilinae), Hydroptilidae and Hydrobiosidae, but surviving on the labial palps of *T. apobamum* (Hydrobiosidae). The Lepidoptera shows the same trend towards reduction of these complexes. They persist on the maxillary palps in Micropterigidae and Eriocraniidae, as well as in Heterobathmiidae (Faucheux 2005, fig. 11). These complexes are absent on labial palps of basal Lepidoptera. The pseudoplacoid sensilla are present in many instances and abundant in Philopotamidae, but they are absent in several families of Integripalpia: Hydroptilidae, Ptilocolepidae, Hydrobiosidae and in *H. acharai* (Rhyacophilidae). The families Stenopsychidae, Hydroptilidae and Hydrobiosidae have reduced or absent groups of long medial chaetoid sensilla on basal maxillary palp segments.

The examinations of *M. maschukella* (superfamily Micropterigoidea) representing the most primitive of the extant members of the order Lepidoptera and *E. cicatricella* (Eriocraniidae, Glossata) (Mitter et al. 2017) have revealed similarities of the lower moths with the Trichoptera. These taxa have almost the same types of sensilla with the addition of peculiar nail- or spatula-shaped chaetoid sensilla on the fifth maxillary palp segments in Micropterigidae, also observed in Heterobathmiidae (Faucheux 2005). The apical sensory complexes in the lower moths are continuous with the rest of the segment, differing in the thinner and either smooth (Eriocraniidae) or ridged cuticle. Labial palps are devoid of this complex. Very large chaetoid sensilla were not observed on basal segments; and blunt chaetoid sensilla are always small and orientated ventrad. Petaloid sensilla in Lepidoptera are found only on labial palps and are grouped sparsely on the apex of the third segment.

The pits with sensilla on palps were mentioned by Martynov (1934) as a characteristic of higher families of Integripalpia. On the contrary, these pits were found in all families of Annulipalpia observed. The pits are nests for the petaloid sensilla. These petaloid sensilla were probably slightly curved and without terminal leaflets at the beginning of their specialisation, each acquiring a more curved shape with a terminal flat extension in the course of evolution. The comparative data on Rhyacophilidae, Hydrobiosidae and the lower Lepidoptera support this hypothesis. The Lepidoptera labial palps have their sensory pits in a subapical position; we consider them as homologues of the pits on the labial palps of Trichoptera, so the straight pore-less basiconic sensilla in Lepidoptera are presumably the homologues of the petaloid sensilla. Comparisons within Lepidoptera (Lastra-Valdés et al. 2020 and citations therein) show the persistence of these pits in recently evolved families, mostly as vom Rath's organs submerged into the third segment. The similarity of sensilla on mouthparts supports the close relationship of Trichoptera with Lepidoptera.

On the other hand, the Mecoptera (Friedrich et al. 2013; Ivanov et al. 2018; Wang et al. 2021, 2022) have limited sensilla diversity. Their mouthparts are provided mostly with simple chaetoid sensilla of various lengths, with rounded flat or concave sensory zones on the palp tips filled with numerous thick short basiconic sensilla, resembling small spheres. Neither petaloid sensilla nor basal swollen segments with long sensilla in groups are found in Mecoptera.

Comparison of sensilla patterns in various caddisfly families suggests a putative ground plan of the palp sensory surface in Trichoptera. Below, we describe the hypothetical set and distribution of sensilla on the ancestral palp segments. Presumably, the initial set of sensory structures for both pairs of palps comprises six types of sensilla: long trichoid, blunt chaetoid, campaniform, mushroom-like, petaloid and thick basiconic sensilla (Fig. 4A).

Maxillary palps (Fig. 4C). The two basal segments of the maxillary palps seem to be shorter than the rest of segments in the Trichoptera ancestor. These segments were covered by a mixture of the trichoid and blunt chaetoid sensilla; the former were more abundant dorsally and inclined towards the palp tip and the latter were concentrated on ventromedial surfaces and were attached at greater degrees to the surface or were almost erect. Lateral, dorsal and ventral chaetoid sensilla were shorter, thinner, less sclerotised (pale) and the medial ones were more sclerotised, larger and dark. The medial large chaetoid sensilla were concentrated at the anterior edge of the first segment; the same sensilla on the second segment occupied completely its ventromedial surface. Longer third and fourth segments had their surfaces covered with inclined trichoid sensilla with the addition of thin blunt chaetoid sensilla on medial and ventral surfaces. The terminal fifth segment was shorter and repeated the pattern of the preceding third and fourth segments for the trichoid and chaetoid sensilla; the apex of this segment had a well-developed apical sensory complex, an attenuated area of thin cuticle without microtrichia forming a cone covered with a few short basiconic sensilla and with larger sensilla on its apex. This attenuated area was the source of the term "Spicipalpia" (Weaver 1984) for what is now understood as the grade of basal lineages of Integripalpia other than subterorder Phryganides (higher Inegripalpia; Thomas et al. (2020)). There was also a sensory subapical field of the petaloid sensilla situated on the dorsolateral surface of this segment, whereas the apical sensory complex, on the

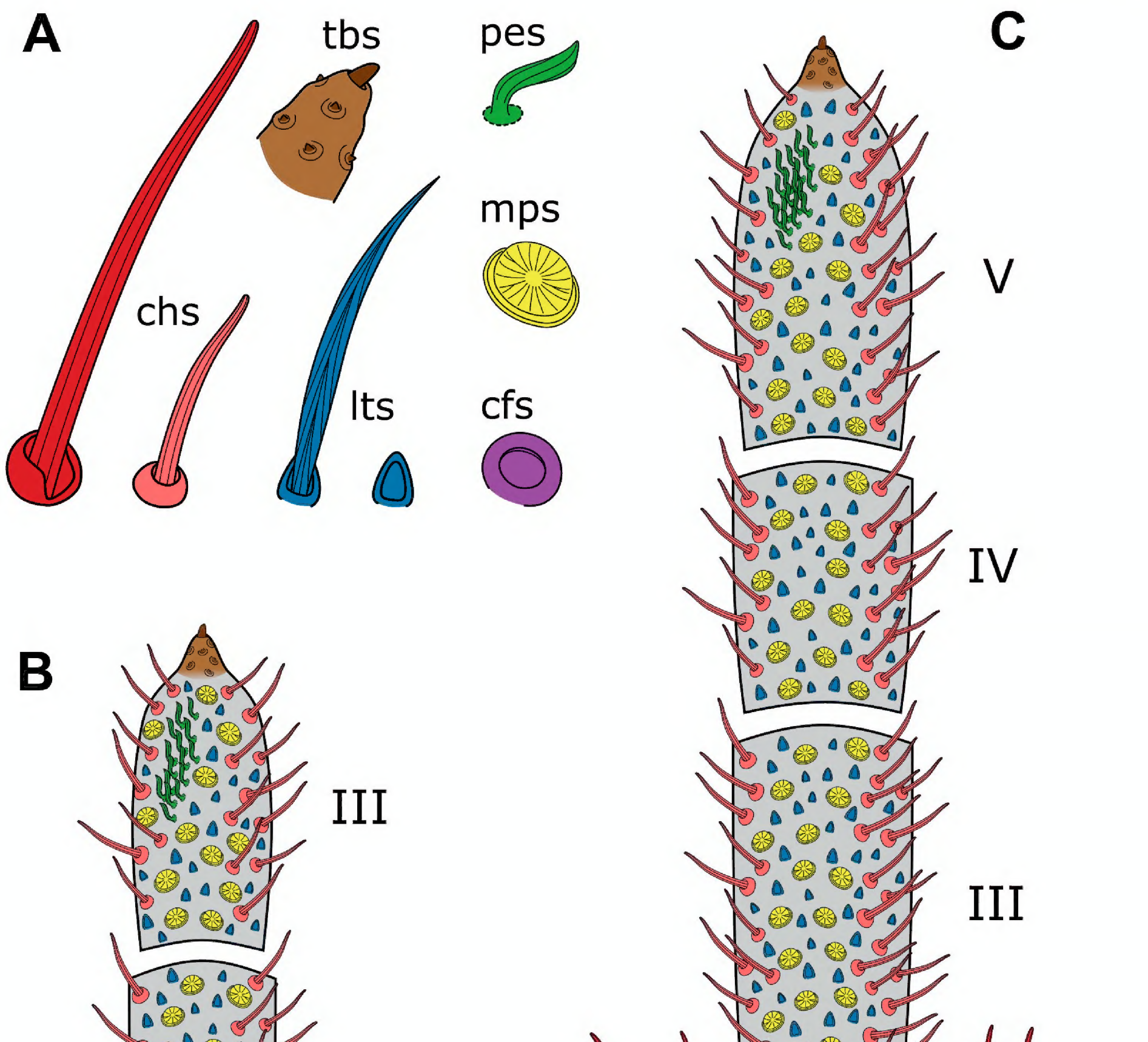

Figure 4. Hypothetical ground plan of sensory surface of labial and maxillary palps in Trichoptera. **A.** Types of sensilla; **B.** Labial palps; **C.** Maxillary palps. Abbreviations: roman numerals = segment numbers; **cfs** = campaniform sensilla; **chs** = blunt chaetoid sensilla; **D** = dorsal surface; **L** = lateral surface; **lts** = pointed long trichoid sensilla; **M** = medial surface; **mps** = mushroom-like pseudoplacoid sensilla; **pes** = petaloid sensilla; **tbs** = thick basiconic sensilla; **V** = ventral surface.

contrary, shifted to a ventral position relative to the axis of the last segment. The mushroom-like pseudoplacoid sensilla with rounded caps were present on the surface of all maxillary palp segments. A few campaniform sensilla occurred on proximal parts of the basal segments.

The ground plan of the sensilla distribution on the labial palps is similar to that on the maxillary palps, with a smaller number of segments (Fig. 4B) and without groups of long stout chaetoid sensilla, but they differed by having trichoid and shorter, pale, slender, chaetoid sensilla. Petaloid sensilla seem to be more abundant than on the maxillary palps, forming a field on the morphologically dorsal surface of the third segment. The apical sensory complex has the same size and structure as on the maxillary palps.

It is likely that palps entirely covered with pseudoplacoid sensilla represent the ancestral character state in Philopotamidae. Ljungberg and Hallberg (1992) reported on the frequent presence of pseudoplacoid sensilla (or "wall-pore sensilla") in various species of some advanced Trichoptera families. If so, a number of basal families show the reduced number of the pseudoplacoid sensilla. In Rhyacophilidae, whose lineage extends to a basal position in recent phylogenetic analyses (Holzenthal et al. 2007a, b; Thomas et al. 2020), the development of pseudoplacoid sensilla is not complete and they are found generally on the fifth segment of maxillary palps and on the third segment of labial palps dorsally.

The ancestral state of sensilla coverage in Amphiesmenoptera might be inferred from the given patterns of the lower Trichoptera and Lepidoptera, considering Mecoptera as an outgroup. The data on sensilla of Mecoptera (Friedrich et al. 2013; Wang et al. 2021, 2022) suggest rather poor diversity, with dominant chaetoid and trichoid elements of different size and, on the apical parts of both palp pairs, very short basiconic sensilla. This Mecoptera condition looks reduced in comparison with other insects. For example, crickets have a large diversity of sensilla on the palps (Klein 1981) with apical pillows subdivided into zones with different sensilla. We consider the rich diversity of sensilla as a putative ancestral character for the Amphiesmenoptera. The set of six principal sensilla types, sensory fields of the petaloid sensilla and modified apical sensory complexes of the two palp pairs with only short basiconic sensilla are apomorphic for Amphiesmenoptera. The presence of pseudoplacoid sensilla is considered also to be apomorphic, because these sensilla are not found on appendages outside Amphiesmenoptera. Hence, the ground plan of the sensilla coverage in caddisflies is similar to the reconstructed ancestral lineage of Amphiesmenoptera. The hypothetical synapomorphic character states of Trichoptera are: (1) greatly enlarged, basal, long chaetoid sensilla on the second maxillary palp segment and (2) a distinct, narrow, apical sensory zone on both maxillary and labial palps. In Lepidoptera, the apical sensory complex of the labial palps has been substituted by a field of petaloid sensilla, developed scales from trichoids and reduced pseudoplacoid sensilla.

Functional interpretation of the sensilla types and the factors of their evolution are very hypothetical until the physiological and behavioural experiments can clarify their specific sensory modes and roles in supporting the sensory input. The hypothetical pre-Amphiesmenopteran ancestor probably had the wider apical sensory zones with various types of longer sensilla to taste the surface of food and, perhaps, the trails and bodies of sex partners. Development of liquid-food feeding decreased the sensory input and the reduced palp apex, bearing a narrow cone-like apical sensory complex, provides sensory input from a small spot. The larger terminal basiconic sensilla of the complex probably could taste a very small area and, by the lateral sensilla, the insect can have additional taste of a droplet where the apical complex is submerged. Frequent use of such a complex needs the permanent presence of the droplets; more dry conditions make it almost unusable in the absence of liquid food. If the adult insect feeds on the sugar substrates from honeydew secreting Hemiptera (Sternorhyncha) excrement or plant fungi, the ventral sensilla scanning the surface in lateral movements will be more adaptive to finding the scattered food and absorbed pheromones. Thus, we can explain the gradual and parallel reduction of these apical sensory complexes in various evolution branches.

Blunt chaetoid sensilla are well developed in lower families of caddisflies, supporting a theory of surface-contact tasting. Some of these chaetoid sensilla changed their sensory input when they became enlarged and sclerotised; these sensilla could taste the chemical signal by contacting the area between the maxillary palps and just beyond the labrum. This signal might be a liquid food droplet capable of being sucked with a short haustellum or it might be some important surface right ahead of the clypeus and between of palps, for example, a body of another individual. This function appearing in the Trichoptera ancestor continues to be important in the lower extant families although it disappears in some more advanced families. These sensilla are movable in one direction and perhaps the insect could move the basal segments up and down while testing.

The pseudoplacoid and petaloid sensilla are hypothesised to be characteristic for Amphiesmenoptera. These short receptors appeared at the earlier stages of evolution and had different evolution trends. Pseudoplacoid sensilla are present on both antennal and palp surfaces, varying in numbers from solitary to very numerous. Antennal surfaces of basal Trichoptera have abundant and diverse sensilla of this type (Ivanov and Melnitsky 2016; Valuyskiy et al. 2017, 2020; Melnitsky et al. 2018, 2019) and the palp segments usually also have them amongst other sensilla, especially on apical segments. Antennae and palps of Lepidoptera have only a few or none of these sensilla (Chauvin and Faucheux 1981; Faucheux 2004, 2005, 2008 and original data). These sensilla on the antennae of *P. montanus* (Melnitsky et al. 2019) have three neurons. The data by Ljungberg and Hallberg (1992) on sensilla histology, suggesting the presence of only one neuron, should be re-examined with modern techniques. If the palp pseudoplacoid sensilla can be shown to have three neurons, they appear to be similar to the coeloconic

thermohygroreceptors of other insects (Altner and Prillinger 1980) also having three neurons. If this assumption is true, the pseudoplacoid hygroreceptor would facilitate the orientation of insects to water; great numbers of these sensilla provide ability to discriminate small humidity gradients produced by open waters, distinguishing them from the noisy background of water vapour from plants and soil. This sensory input provides orientation for water to find a habitat for egg laying and partner finding. Species of Trichoptera like *Thamastes dipterus* Hagen (Apataniidae) that mate on the water surface without a vapour gradient, have a small number of these sensilla on their antennae (Valuyskiy et al. 2020). The lower Lepidoptera have no need of open water and lack pseudoplacoid sensilla. Development of these sensilla in the probable Amphiesmenoptera ancestor suggests its dependence on humidity or even the shores of lakes or rivers. The subsequent fate of these receptors is different in caddisflies and moths: the former are very dependent on their input for orientation in most species and the latter do not need them.

Petaloid sensilla are persistent on palps of Trichoptera and on labial palps of Lepidoptera. More-recently evolved Lepidoptera species have the vom Rath organ on their labial palps as a bundle of peg-like petaloid sensilla in a deep socket (Lastra-Valdés et al. 2020). These sensilla have been shown to be responsible, in three species of *Rhodogastria* (Noctuidae), for the reception of CO_2 and, with lesser sensitivity, for some volatiles like limonene and citral produced by plants (Bogner et al. 1986). The petaloid sensilla of Trichoptera were originally situated on the dorsal surfaces of palps and probably are responsible for the same types of reception. Additionally, their position in pits resembles that of vom Rath's sensilla. The reception of pheromones also is a possible function of these sensilla.

The results of our comparative investigation of palp sensors show significant similarity of types and distribution patterns in lower Trichoptera. The trends in evolution of sensilla patterns in basal caddisfly families are present as reductions of the certain sensory structures at the apical and basal parts of palps. Our comparison with Lepidoptera suggests differences in the evolution trends in Trichoptera and Lepidoptera and presence of patterns related to the ancestor of Amphiesmenoptera. We predict that the sensilla of palps might be useful for the taxonomy of caddisflies. Subsequent studies of the more-recently evolved Trichoptera will uncover patterns of sensilla evolution in those taxa.

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